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FOOD WEBS AND PRIMARY PRODUCTION IN THE BARENTS SEA

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Abstract: This summary paper describes the food webs in the Barents Sea and deals with the seasonal changes in the phytoplankton stock and productivity. The pelagic food web is, as elsewhere, based mainly on unicellular algae (phytoplankton) as the primary producers. Temperatures of −1.8 to 5°C set an upper limit of about 0.6–0.8 d^{-1} for the growth rate of diatoms in the Barents Sea. Phytoplankton biomass may reach as high as 10–15 mg m^{-3} in terms of Chlorophyll *a* or 300–600 mg m^{-3} in terms of carbon at the peak of the spring bloom. During most of the productive season, Chl *a* concentrations are 0.2–1.0 mg m^{-3} in the upper layers and 5–20 mg m^{-3} at and near the pycnocline. Typical daily rates for primary production are 10–60 mgC m^{-3}; during the peak of the spring bloom up to 300–600 mgC m^{-3}.

1. Introduction

The Barents Sea covers about 1.4×10^6 km^2, of which about half is covered seasonally by ice. Multiyear ice occurs usually in the form of scattered chunks which have been introduced from the Polar Basin. The Barents Sea is a shelf sea; depths are mainly between 200 and 400 m, although some banks are as shallow as 40 to 100 m (the Svalbard Bank and the Central Bank). The southern half of the Barents Sea is characterized by Atlantic water masses with a temperature of 3–6°C. At the Polar Front (at about 76°N), Atlantic water descends under a layer of Polar water, which is lower in temperature (down to the freezing point), yet lighter because of its low salinity relative to Atlantic water. The Polar Front is relatively well-defined in the western part of the Barents Sea, while there is a broad zone of mixing in the eastern half. North of the Polar Front the productive season (March–October or shorter, depending on how long the waters stay open) is characterized by the light Polar water overlying the Atlantic water and a most accentuated pycnocline between the two water masses—usually at 20–40 m depth. South of the Polar Front mixing characteristics are most variable, depending on wind and currents, not to mention the occurrence of banks and islands. Near the Svalbard Bank waters are, for instance, thoroughly mixed the year round.

This paper deals with some of the basic features of the ecosystem in the Barents Sea and is a brief synopsis of some of the knowledge accumulated by many colleagues in Pro Mare (The Norwegian Research Program for Marine Arctic Ecology). Comprehensive information will be published in several papers of the Proceedings of the International Pro Mare Symposium on Polar Marine Ecology held in Trondheim, Norway,

12–16 May 1990. Reviews of the Barents Sea ecosystem dynamics have been published elsewhere (SAKSHAUG and SKJOLDAL, 1989; SAKSHAUG, 1989), and contain essential references. Unpublished recent information on the Barents Sea necessary for the present synopsis has been made available by H. LOENG, F. MEHLUM, F. REY, D. SLAGSTAD, T. F. THINGSTAD and P. WASSMANN (fish, seabirds and marine mammals, phytoplankton, macrozooplankton, the microbial loop and sedimentation, respectively) for which they are gratefully thanked.

2. The Food Webs in the Barents Sea

The marine grazing food web in the Barents Sea may be divided into three parts, of which the benthic web will not be dealt with here (Fig. 1). The other consists of the ice biota, starting with ice algae, followed by ice fauna (mainly amphipods), then seals (mainly ringed seals) and, finally, polar bears. The third, the pelagic food web, is based on phytoplankton which in turn are grazed by zooplankton (mainly copepods and krill) and which again are eaten by fish—in the Barents Sea pelagial mainly capelin. The capelin is a key species in the Barents Sea in the sense that both cod, seabirds, seals, whales, and man compete for it. It thus plays a role similar to that of krill in the Antarctic Ocean.

Energy and matter are fixed by the primary producers, and both flow through the ecosystem. Transfer between trophic levels takes place each time one organism eats another. As a rule of thumb, transfer from one trophic level of the system to a higher one implies a loss of 80% or more of the energy and similar losses of matter. At each

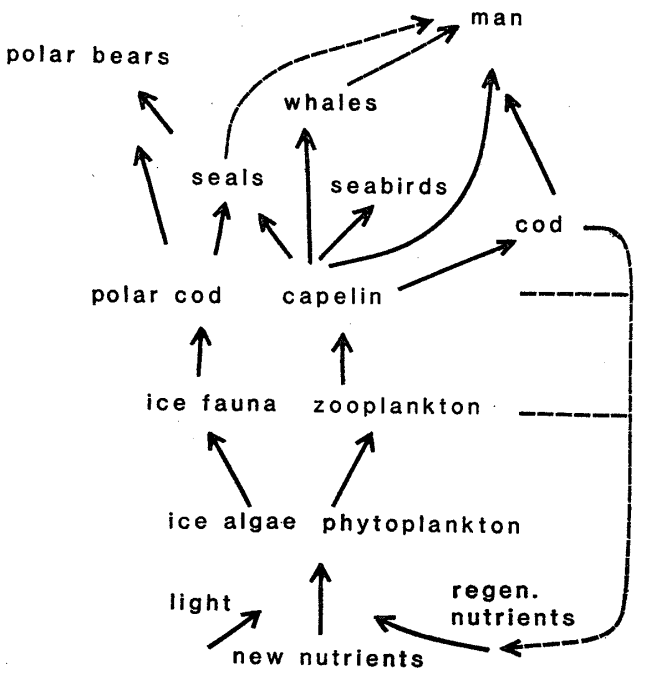

Fig. 1. Food webs in the Barents Sea: ice biota (left half), pelagic system (right half).

trophic level, the bulk of energy and matter is spent on maintaining life, on feeding forays, on reproduction, etc. Energy is dissipated, while matter (nutrients) excreted by organisms may be reused by phytoplankton. With such large losses in each transfer, the food web can hardly have more than 5–6 trophic levels.

Apart from the grazing food webs depicted above, the "microbial loop" may play a prominent role. Marine bacteria may take up nutrients in the water (and thus compete with phytoplankton) or they may graze organic matter, for instance remains of other organisms. The bacteria may in turn be destroyed by virus (BERGH *et al.*, 1989) or eaten by various non-photosynthetic microflagellates, which in turn may be eaten by various microzooplankton, *e.g.* ciliates. Flagellates may excrete significant amounts of nutrients which are reused by bacteria or phytoplankton, while a fraction of the ciliate stock may be eaten by larger zooplankton; thus some of the energy and matter may be transferred to the grazing food web.

For each trophic level we have that, neglecting lateral and vertical transport of organisms,

$$dB/dt=(\mu-d)B \qquad (1)$$

where dB/dt is the time-dependent change in biomass, μ is the specific growth rate, and d is the death rate. By coupling the equations for each trophic level and describing the rates as a function of environmental variables, a dynamical ecosystem model can be constructed. Equation (1) states that the change in biomass with time is a function of the difference between the growth rate (gain) and the death rate (loss). Logically, environmental variables first affect the rates, and changed rates then affect the size of the standing stock. Thus changes in standing stocks are secondary effects of the environmental impact. The predictive power of a model regarding changes in standing stock thus depends on good measurements of the environmental variables and precise knowledge about the mathematical relationship between these variables and the relevant rates. We know, however, more about standing stocks in an ecosystem than these rates: some of the latter are notoriously difficult to measure, in particular loss rates. Then, however, we cannot decide the cause/effect relationships: did a standing stock decrease because the growth rate decreased or because the death rate increased? Such questions are urgent concerning the management of biological resources in the Barents Sea and certainly have political implications; man affects the death rate of some stocks through harvesting.

In the very long-term sense (many years) growth rates may equal death rates, *e.g.* the ecosystem is close to steady state. In the short-term sense, however, polar marine ecosystems are far from equilibrium; standing stocks thus fluctuate markedly, as should be expected from the large seasonal and year-to-year fluctuations in environmental variables. The frequently used term "ecological balance" in conjunction with such systems is therefore highly misleading and relevant only in the context of average properties over many years.

It so happens (albeit with prominent exceptions) that the lower the trophic level, the larger the standing stock and the higher the growth rate. It is, however, notoriously difficult to estimate the "average" long-term biomass for different trophic levels; besides, such averaging neglects the extremely high variability from one season to another, from

one year to another, and the fact that a major fraction of the biomass may be unevenly distributed and concentrated near the ice edge. Allowing for wide margins of error and assuming that at least the relative difference between stock sizes of different trophic levels is adequately illustrated, I have made such an attempt (Table 1), which shows that in the Barents Sea there is on the average more zooplankton than phytoplankton present (3 *vs* 2 tonnes of carbon per square kilometer, *e.g.* the biomass pyramid is inverted). This is rather typical in the oceans, but the production (biomass times growth rate) pyramid is of course not inverted, because of the much lower growth rates of zooplankton relative to phytoplankton. Higher up in the system, standing stocks are much lower. Average stocks of capelin and cod, for which there is a fair amount of data, represent about 400 and 300 kgC km^{-2}, respectively. Data for these stocks reflect, however, how extreme variations in stock size are between years. At present, the capelin stock in the Barents Sea is at a low, *e.g.* <100 kgC km^{-2}, while it in good years may reach up to 700 kgC km^{-2}. The cod stock varies in a less extreme fashion; nevertheless a range from 150–700 kg carbon per square kilometers must be considered wide. Even if the Barents Sea is considered a very rich area in terms of seabirds, they do not represent more than about one kilogram of carbon per square kilometer, and the polar bear, the top predator, represents about 70 grammes of carbon per square kilometer. Still, polar bear populations are considered to be about as large as the local food supply allows. For comparison, the population density of Norway and Japan corresponds to about 80 and 1600 kilograms of carbon per square kiometer, respectively.

Table 1. Average population density of some important trophic constituents in the Barents Sea (kgC km^{-2}) and scale of generation time.

	Biomass	Generation time
Bacteria	400	hours–days
Phytoplankton	2000	days
Macrozooplankton	3000[1]	months–2 years
Capelin (*Mallotus villosus*)	400[2]	1–4 years
Cod (*Gadus morthua*)	300[3]	several years
Whales	20	several years
Seals	11	several years
Seabirds	0.75	several years
Polar bears	0.1	several years
Man (in Norway)	80	several years
Man (in Japan)	1600	several years

Population density of Norway and Japan is given for comparison. Calculations are based on information provided by H. LOENG and F. REY, The Institute of Marine Research, Bergen; F. MEHLUM, The Norwegian Polar Research Institute, Oslo; T. F. THINGSTAD, University of Bergen; D. SLAGSTAD, Automatic Control, SINTEF, Trondheim; as well as own data.

[1] *Calanus* spp. and krill.

[2] variation between years: 30–700.

[3] variation between years: 150–700.

3. The Annual Phytoplankton Cycle

For a phytoplankton bloom to start, there has to be an ample supply of both plant nutrients and light. The ambient nutrient concentration depends on the difference between supply and consumption by algae and bacteria. In winter, the consumption of nutrients by phytoplankton is negligible, therefore concentrations of nutrients in the upper layers remain at the high level which is typical for the deep water. Winter concentrations in the Barents Sea are about the same as for the Northeast Atlantic in general: 9–14 mmol m^{-3} of nitrate, 0.5–0.6 mmol m^{-3} of phosphate, and 4–5 mmol m^{-3} of silicate. There are only traces of ammonium in winter because of little biological activity. These figures are among the lowest for polar seas. There are about twice as high winter concentrations of nitrate and phosphate in the Bering Sea and even somewhat more in the Antarctic Ocean. The ratio between nitrate and phosphate is, however, the same in the three areas: *e.g.* about 16 (atoms). Silicate concentrations are about 7–8 times higher in the Bering Sea than in the Barents Sea, and as an average about 20 times higher in the Antarctic Ocean (about 100 mmol m^{-3}). These regional differences may be related to the age of deep waters, *e.g.* the waters in the Northeast Atlantic may reflect that the Norwegian Sea produces its own bottom water which thus is young and little enriched.

During March–July, depending on ice cover and the depth of vertical mixing, the spring bloom starts and rapidly consumes the winter nutrients in the upper layers. Growth rates may reach up to 0.6 d^{-1} at −0.5°C (GILSTAD and SAKSHAUG, 1990) and possibly to 0.8–1.1 d^{-1} at 3–6°C. In the southern half of the Barents Sea, where waters are permanently open, this bloom takes place in late April or May. If waters are stable and the pycnocline situated not deeper than 20–30 m, light conditions are very favorable. This ensures rapid exponential growth and a short duration of the bloom—possibly less than two weeks—because it cannot develop beyond the point of depletion of the winter nutrients. If the vertical mixing reaches 50–60 m depth, the start will be delayed, possibly by a week or two; it will develop slowly, and perhaps last for a month. Obviously, a major fraction of the primary production during the spring bloom is "new".

The duration and timing of the spring bloom relative to the development of zooplankton (match/mismatch) is of major ecological interest. When the nutrients in the euphotic zone have become consumed, mass sinking of phytoplankton takes place unless grazers in the upper layers remove a significant fraction. Evidently there is a greater chance of match between phyto- and zooplankton if the spring bloom is of long duration and if it is late than very early. It is obvious that questions related to match and mismatch are crucial for the understanding of the fluctuations in zooplankton and possibly fish stocks; on the other hand such studies require a very large and expensive data base.

Judging from the loss of nitrate in the upper 100 m in spring, the conversion of new nutrients into biomass during the spring bloom may represent up to 60 gC m^{-2}. However, only about 1/3 of this biomass is actually observed during the early phases of the bloom—the remaining biomass sinks out of the euphotic zone or is grazed. Towards the end of the bloom more than 90% of the produced carbon has sedimented or

become grazed. In the northern half of the Barents Sea, where Polar water is prevailing, mixing is shallower, and the total conversion of new nutrients during the bloom may not represent more than about 30 gC m^{-2} in terms of biomass. The sinking fraction of the spring bloom biomass may typically constitute 50–80% of the total. A major part of this fraction feeds the benthic fauna, which thus gets one albeit large meal per year. Another fraction, possibly small, may be stored in the longterm sense as sediments. This fraction is of climatological interest in that it may represent long-term storage of carbon.

Ice cover, mainly in the northern half of the Barents Sea, affects the development of the spring bloom. It is opaque enough (particularly because of snow) to prevent growth of algae in early spring in the waters under the ice (but not necessarily growth of algae attached to the under-side of the ice). Thus the winter concentrations of nutrients in waters under the ice are apparent until the ice melts. When the ice melts—north of the Polar Front due to seasonally increased radiation—the rather fresh melt-water mixes with the salt water and forms a stable upper layer and a pycnocline as high up as 20–30 m. Thus, when the ice melts, both light and nutrients are suddenly present in ample supply, and a spring bloom starts almost explosively. While the ice edge retreats northward towards summer, ever exposing new nutrient-rich water masses to strong light, the ice edge bloom trails it as a band of 20–50 km width. Therefore a large portion of fish, seabird and seal stocks are attracted to the ice edge zone. To the extent the ice edge is well-defined (which it often is not), the ice edge bloom may be regarded as a belt of concentrated biomass which sweeps the Barents Sea during the first half of the growth season (Fig. 2). The farther north, the later the phytoplankton bloom and the shorter the growth season. This scenario has been verified for all polar seas and was first proposed by GRAN (1931).

The maximum phytoplankton biomass during the spring bloom in the Barents Sea is 10–15 mg m^{-3} in terms of chlorophyll *a*, or 300–600 mg m^{-3} in terms of carbon. The prevailing maximum growth rates then set an upper limit for the primary production

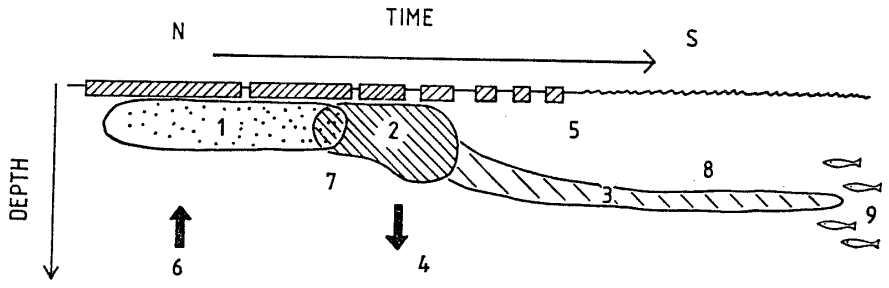

Fig. 2. Schematic picture of the seasonal plankton development in the Barents Sea. The receding ice edge acts as a biological time-setter, and various stages of the seasonal plankton development can be found along a North-South gradient. 1: Prebloom phytoplankton growth, 2: Ice edge phytoplankton bloom, 3: Post-bloom deep chlorophyll a maximum, 4: Sedimentation of phytoplankton, 5: Oligotrophic post-bloom surface layer, 6: Upward migration of overwintering zooplankton, 7: Spawning of zooplankton, 8: Development of new generation of zooplankton, 9: Capelin feeding migration. (F. REY, H. R. SKJOLDAL and A. HASSEL, unpublished)

rate for particulate carbon of 180–480 mg $m^{-3} d^{-1}$ during the peak of the spring bloom.

After the winter nutrients have been consumed, further growth is regulated by the immediate nutrient supply. In the northern half of the Barents Sea where a pronounced pycnocline remains until the end of the growth season, transport of new nutrients to the upper mixed layer is at a minimum. Therefore, the primary production in this layer is largely regenerative: the algal biomass is low (0.2–1.0 mgChl *a* m^{-3}), and the microbial loop plays a prominent role. With little new production, sedimentation is presumably of little significance. At and right below the pycnocline there is, however, a marked maximum layer of phytoplankton in terms of Chl *a* (at times up to 20 mg m^{-3}). To some extent this maximum reflects that algae are shade-adapted (rich in Chl *a* and growing slowly, *e.g.* about 0.1–0.2 d^{-1}), but it is also evident that the Chl *a* maximum layer has a biomass (in terms of carbon) several times that of the mixed layer above. The primary production rate may be about the same in the two layers and may total 10–60 mgC $m^{-3} d^{-1}$.

In the southern half of the Barents Sea a number of processes ensuring further supply of new nutrients after the spring bloom may take place: pycnoclines are weak enough to be eroded by wind-induced mixing, there may be local upwelling events induced by wind, there are shear forces between currents, and there are island and bank effects (erosion of pycnoclines due to bottom topography). At the very shallow Svalbard Bank, waters are well mixed to the bottom the year round, but the area is too shallow for mixing to prevent high primary production. Altogether, it is likely that the total primary production is higher in the southern than in the northern half of the Barents Sea, and certainly the fraction of new production is higher.

Vertical mixing is a double-edged sword: on one hand it is essential for the supply of new nutrients to the euphotic zone; on the other hand it ruins the light regime for the algae. RILEY (1963) put forth the idea that the ideal condition with respect to maximizing of the primary production might consist of alternating turbulent and stable regimes. The first would bring up new nutrients, the other would furnish light (stability). We might imagine that passing atmospheric low pressures may create this type of situation: strong wind in front of the center, stability after its passage and before the arrival of the next low pressure. Satellite imagery of Chl *a* in the Norwegian Sea in combination with meteorological data might reveal if this scenario is realistic.

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